

EXPANSION OF RANGE OF THE SPECKLED WOOD BUTTERFLY, *PARARGE AEGERIA* L., IN NORTH-EAST SCOTLAND

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Introduction

Thomson (1980) in an exhaustive treatment of the past and present distribution of Scottish butterflies, showed that several of our species have not only maintained but increased their ranges in recent years. That this is in strong contrast to the unhappy situation in many parts of England is confirmed by the account of Heath *et al.* (1984). One of the notable 'success stories' among northern butterflies has been that of the speckled wood *Pararge aegeria*. A few years ago restricted to a small area on the Atlantic coast of west Scotland, it has expanded both northwards and southwards, into areas from which it had previously been absent since the late nineteenth or early twentieth century (Downes 1948). Still more remarkably it has recently invaded a large area of coastal north-east Scotland where there is no evidence that it ever occurred before. This paper chronicles the history of that invasion and attempts to answer some of the ecological questions that it poses.

The pattern of expansion

1. Early years (Fig. 1). The first record of the butterfly was that of Davidson (1956) who caught a single tattered female at Dochgarroch, about 3 miles south-west of Inverness, on 14.viii.55. This individual was nearly 60 miles from the then known distribution area of *aegeria* on the west coast, and Davidson suggested that it might have been a vagrant from there, transported by strong south-west winds.

No further record is extant until Mr. B. Morrison observed *aegeria* in conifer woodland at Dalcross 8 miles east of Inverness on 6.vii.61. On this occasion 2 butterflies were seen, clearly not vagrants but part of an established population.

These two records constitute the only evidence we have of the eastern population in those early years. Taken in conjunction (and in the context of an area then poorly recorded for Lepidoptera) they seem to indicate a population occupying a quite compact area (perhaps 100 square miles) within a few miles radius of the town of Inverness.

2. 1969-72 (Fig. 2). Hulme (1969b) reported finding several of the butterflies at a spot near Munloch on the Black Isle (in fact

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a broad peninsula at the inner end of the Moray Firth) on 27.vii.69. Mr. D. C. Hulme, an experienced and active lepidopterist resident in the area since 1963, had not previously seen the species anywhere in east Inverness-shire or Easter Ross. I am indebted to him for details of his further sightings which followed in the next 3 years. In 1970 the Munlochy colony was again flourishing. In 1971 the species appeared further north in the Black Isle at Rosemarkie, and in a new site east of Inverness at Cawdor. In 1971 Dr. R. Richter also saw the first *aegeria* in the western end of Culbin Forest, an extensive area of mature pine forest on coastal sand dunes east of Nairn. Next year (1972) the butterflies were reported in several parts of Culbin Forest, right to its eastern end on the shore of Findhorn Bay (BRC). In 1972 Mr. D. C. Hulme also found new localities at Cromarty (the northern point of the Black Isle) and several miles inland to the south-west at Glen Affric.

In the space of about 4 years the population appeared to have achieved a major expansion from its original base: taking Inverness as the point of origin it had now travelled some 27 miles ENE to Culbin Forest: 17 miles NNE to Cromarty: 27 miles WSW to Glen Affric. The total distributional area now occupied was of the order of 400 square miles.

3. 1973-78 (Fig. 3). In this six-year period there were significant further advances northwards, southwards and eastwards from the area occupied in 1972. The movement was constrained by the topography of the area into definite corridors of advance, as the butterfly seems effectively restricted to land below about 250m. One corridor lay along the coastal plain of Morayshire: one across the Tain peninsula of Easter Ross: and another inland to the Great Glen along the shores of Loch Ness.

The colonization of Culbin Forest was followed by progress inland to Darnaway Forest in 1975 (Dr. R. Richter) and Vale of Pluscarden in 1977. Along the coast *aegeria* appeared in Roseisle Forest (1976) and Oakenhead at the west end of Lossie Forest (1978). The rapid spread across the 'Laich' or plain of Moray was undoubtedly favoured by the high proportion of this area occupied by mature Scots pine forest (see below).

South of Inverness the butterfly's progress was followed by Mr. D. B. McGinn who found it at Loch Ashie in 1978 and at the Scottish Wildlife Trust's Farigaig Nature Reserve in 1977. Westwards there was a limited amount of penetration into the Ross-shire Glens: Mr. D. C. Hulme saw 3 in the Contin/Strathpeffer area in 1975.

In 1978 Mr. C. Headlam saw the first *aegeria* in his garden at Fearn near Tain. Further north still the butterfly appeared in woodland on the north side of Struie Hill (BRC) showing that it had

then gained access to the sheltered, well-wooded district of the inner Dornoch Firth.

Allowing for some inevitable gaps in recording, it can be calculated that the distributional area occupied to 1978 inclusive was around 750 square miles. The maximum distance travelled from the supposed origin point at Inverness was 40 miles (Oakenhead).

4. 1979-84 (Fig. 4). These 6 years saw further rapid expansion in the eastward direction, less to the south and west where the more unfavourable habitats of the high glens and mountains impeded progress.

From its 'bridgehead' at Oakenhead the butterfly spread eastwards through Lossie Forest to the area around the mouth of the River Spey. The first record east of the Spey was near Fochabers on 17.viii.80 (Dr. R. Richter). From here it progressed rapidly to colonize the large area of conifer woodland in Speymouth Forest (1981). At the same time it was striking inland around Elgin and I found it in pinewoods at Longmorn and Birnie for the first time in 1981. Mr. S. North found it in alder woodland at Rothes on the Spey in 1982, the furthest inland it had so far been seen in this eastern 'limb' of the distribution.

1983 saw the first records in Banffshire, near Mulben and at Bauds Wood near Portknockie. After a seeming deceleration during 1981-82, the coastal advance continued with renewed speed and in 1984 I found it in woodland just outside Cullen and at two different sites near Portsoy. These Portsoy records make the total distance travelled from *aegeria's* point of origin at Inverness to be 62 miles. In 1984 the butterfly was also consolidating its inward spread up the Spey: I found it in 3 different sites around Rothes and Dr. Richter saw it a further 9 miles upstream at Boat o' Brig.

In the western part of the range, there was some consolidation but little in the way of further spread. New records in this period included mid-Loch Ness 1979 (BRC), Strathconon 1980 (Mr. G. Thomson), and Glen Strathfarrar N.N.R. 1982 (Mr. H. Brown). No further movement to the north was reported: this may simply reflect lack of recorder coverage, but it may be significant that the northernmost record at Struie Hill (1978) is close to the latitude of *aegeria's* northern limit on the west coast too.

The further substantial increase in range in the period 1979-84 has brought the total distributional area of the butterfly in north-east Scotland to around 1,000 square miles. Further rapid expansion may be anticipated and it is very likely that 1985 or '86 will see the spread of the butterfly both northwards into Sutherland and eastwards into Aberdeenshire.

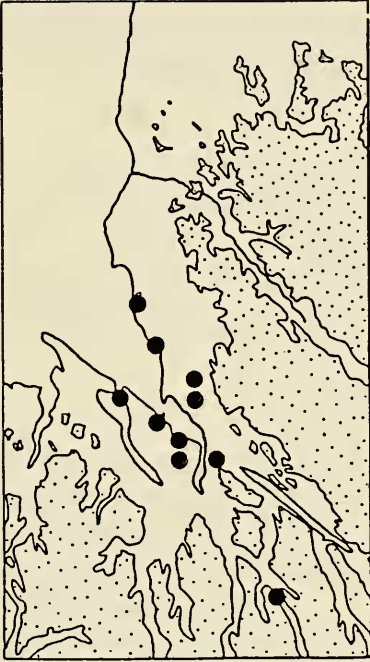


Fig. 2 up to 1972

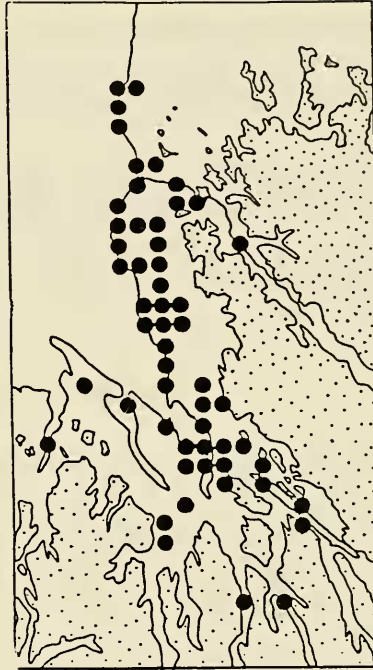


Fig. 4 up to 1984

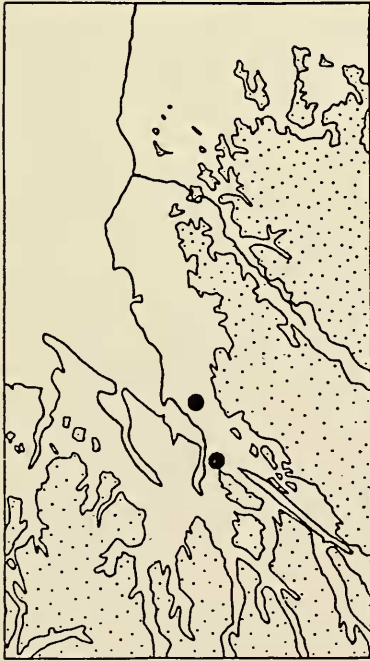


Fig. 1 up to 1966

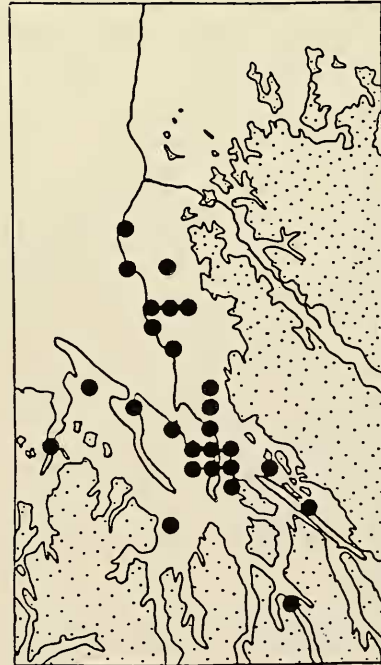


Fig. 3 up to 1978

Figures 1 to 4 : Distribution records of the speckled wood plotted cumulatively over 4 successive periods. The records are plotted on 5 x 5 km squares. Land areas over 250 m are shaded.

Discussion

The above outline of events over a period of approximately 30 years (1954-84) raises a number of ecological questions as to underlying reasons and mechanisms:—

- 1) How was the population in north-east Scotland initiated?
- 2) Why was there such a long time between the first record (1955) and the start of the period of rapid expansion?
- 3) What has driven the rapid and progressive spread, at a seemingly fairly steady rate of 3-3½ miles per year, from 1969 onwards?

Founding of the population

The appearance of the present-day distribution map of *P. aegeria* (Heath *et al.* 1984) shows that the north-eastern distribution is almost continuous with the range of the butterfly on the west coast of Scotland, the minimum distance between them being about 22 miles in the area of the Great Glen. From this it seems natural to suppose that this north-east population arose by spread from the west coast, through the narrow glens of the northern highlands, to reach the area of the inner Moray Firth some time in the early nineteen-fifties.

However, the detailed evidence that we have suggests that this was not the case. First, the two mutually-supporting early records (1955, 1961) were only 10 miles apart, close to the town of Inverness and at the very centre of the population's subsequent expansion (Figs. 1-4). This in itself suggests that the population originated there, either by accidental or perhaps human introduction some time prior to 1955. Secondly, the negative evidence: the effective restriction of the butterfly to ground under 250m means that there are only two narrow corridors through which it could have spread from the west, one up the Great Glen and one further north through Glen Carron and Strath Bran. There are no records at all for the latter area, while in the Great Glen itself there are no records prior to that at Farigaig (1977). Again, the detailed account by Howard (1978) of the macrolepidoptera of Glengarry omits any mention of *aegeria* there, indicating a real gap in the species' distribution.

The balance of evidence seems strongly in favour of a single point of origin, close to Inverness, nearly 60 miles from the west-coast range of *aegeria* at that time. Although Thomson (1980) provisionally assigned the new population to the west-coast race *oblita*, it cannot be certain whether the first introduction involved stock of western Scottish origin or perhaps from a more distant source. It may be relevant to recall that Hulme (1969a) found a

single specimen of *Celastrina argiolus* in the Black Isle in 1966, a species whose British distribution is otherwise confined to England and Ireland.

'Latent period' between 1955 and 1969

There is a strong contrast between the apparent slowness of population spread in these early years and the subsequent rapid advance illustrated in Figs. 1-4. In quantitative terms it seems that in the 15 years 1954-69 the butterfly must have spread by less than 1 mile per year on average: in the 15 years 1969-84 it achieved a fairly steady rate of just over 3 miles per year.

Reasons for this slow start might lie in the genetic structure of the population. The initial very small population (perhaps even arising from a single fertilized female) would be expected to have a greatly impoverished gene-pool, and one which was perhaps quite atypical of whatever parent population it had arisen from. This is the so-called 'founder principle' (Ford 1971 pp. 42-45) which has important implications for the evolution of small isolated populations. An iso-enzyme study, along the lines of that of Handford (1973) for *Maniola jurtina* might throw much light on this question, and also the question discussed above as to the geographical origin of the founding population. Again, a very small founding population (particularly if deriving from a single female founder) would be expected to suffer from inbreeding depression. The adverse effect of deleterious recessive genes which become exposed in such a population can decrease viability for a number of generations.

However there is a much simpler explanation which can be advanced for the apparent slowness of spread in the early years. This is just that a very small population spreading from a single nucleus takes much longer to advance a given distance than a large population multiplying at the same rate. For example, suppose that a founder population occupied an area of only 0.01 square miles and doubled in numbers (and so in area) each year. After 15 years the area occupied would be 328 square miles but the distance moved from the point of origin would be only 10.2 miles (assuming a circular dispersal). Further doubling would result in an ever-increasing rate of (linear) spread through time: however this is unrealistic in view of the limited powers of dispersal of the 'excess' population. Given that only the peripheral part of an expanding population is likely to be capable of colonizing new territory, the rate of advance is expected to approach a limiting value, proportional partly to the rate of population increase and partly to the distance of movement of colonizing individuals. This is what seems to have happened in the case of *P. aegeria*'s eastward spread since 1969.

Reasons for the rapid spread 1969-84

To some extent this question has just been answered by supposing a rapid rate of population increase (perhaps twofold) and a limited power of dispersal of colonizing individuals (perhaps 3-4 miles). It seems the butterfly produces more than one generation per year, although the exact sequence of broods is given conflicting interpretations by different authorities (Heath *et al.* 1984). The usual pattern in northeast Scotland is for a small spring brood in May-June, a large main brood in July-August and a very small (sometimes lacking) autumn brood in late September-October. It will be appreciated that even partial double-broodedness can greatly enhance the population's rate of increase and spread.

The reason for the rapid increase itself we can only guess at. It is clear that *aegeria* has been invading a vacant ecological niche in this part of Scotland: no other butterfly is adapted for life in the dense shade of mature woodland which it favours. It seems to have undergone something of a habitat shift at the same time. Thomson (1980) referring chiefly to the west coast Scottish population, gave its habitat as 'deciduous woodland'. Two of the first three records from the north-east were also in deciduous woodland: Dochgarroch 1955, in oakwood and Munloch 1969, in beech. However, of 18 sites where I myself found the butterfly during 1976-84 no fewer than 14 were exclusively mature conifer woodland, usually of Scots pine. Responses to a request for information which I placed in local newspapers confirmed this habitat preference. (In most of *aegeria*'s Scottish west coast range the predominant conifer woodland is spruce not pine. Spruce plantations are generally so dense as to be very deficient in ground flora, so lacking the abundant supply of grasses such as *Dactylis glomeratus* and *Agropyron repens* on which *aegeria* feeds.) The butterfly has successfully colonized mature pine woodland of a similar character in the Breckland district of East Anglia (Heath *et al.* 1984). Elsewhere its present-day distribution anywhere on the east coast of Britain is extremely sparse. Lees (1962) considered that *aegeria* was restricted climatically to areas having relatively high temperatures in winter and high night temperatures in summer. It may be that a minor evolutionary shift in the population of the Moray Firth area of Scotland has enabled it to escape this climatic restriction, and so to take advantage of the exceptional concentration of mature pine woodland which characterizes this area.

Summary

The distribution of the Speckled Wood in north-east Scotland has been expanding steadily for about 30 years since its first appearance near Inverness. Rate of spread was slow in the early years

but later increased to over 3 miles per year in favourable habitat. The butterfly seems to have exploited a previously vacant niche in the extensive mature pinewoods of the area.

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